

Where and When Might the Tropical Angiospermous Flora Have Originated?

by

ROBERT F. THORNE

Rancho Santa Ana Botanic Garden, Claremont, California 91711

Summary

The tropical angiospermous flora had its beginnings with the origin of the angiosperms in earliest Cretaceous time from some unknown, generalized gymnospermous ancestor, probably a still unrecognized group of Mesozoic pteridosperms. Over most of early and middle Cretaceous time, the angiosperms, early split into dicots and monocots, gradually became more prominent in tropical and later in temperate floras, with evolution by late Cretaceous in part into extant families and genera. The facts of present and past angiosperm distribution still point to southeastern Asia and attendant archipelagoes as the primary centre of preservation and probably the primary centre of origin of the most primitive living angiosperms. Other important centres for the development of the tropical angiosperm flora have been West Gondwanaland before its break-up, the upland shield areas of South America and Africa since their isolation from one another, Australasia, and to a much lesser extent the Greater Antilles and Mexican highlands.

Introduction

The origins of the angiosperms are still obscure. When, where, and from what ancestral group they originated are still matters of much speculation and disagreement. We are much better supplied with negative information than with positive facts due to the incomplete nature of the fossil record and the almost universal extinction of the earliest angiosperms and their probable ancestors. However, expanding knowledge about the class Angiospermae enables us to narrow down considerably our choice of answers.

Antiquity of the Angiospermae

The earliest guesses about the antiquity of the angiosperms were rather wild, ranging from the Cretaceous back at least to the Permian of late Paleozoic time. The earliest indisputable angiosperm remains, monosulcate angiosperm and tricolpate pollen, appeared in the fossil record in Barremian and Aptian time of the Lower Cretaceous less than 130 million years ago (Doyle, 1969, 1973; Wolfe *et al.*, 1976). Earlier fossil remains claimed to be angiospermous have been eliminated from consideration as belonging to other vascular plant classes or as having come from more recent strata than those to which they were first assigned (Scott, Leopold, and Barghoorn, 1960; Scott *et al.*, 1972). The complete absence of unequivocal angiosperm fossils from strata earlier than the Barremian, or possibly the Hauterivian, makes it gratuitous to assume a much earlier Jurassic or even Triassic origin for the angiosperms.

Gradual Emergence of the Angiospermae

Another myth like early Mesozoic origins that should be set aside permanently for the early angiosperms is that they burst full-bloom in great numbers and variety upon the Early Cretaceous scene. We have enough fossil floras analyzed now that we can say categorically that the angiosperms very slowly gained prominence in

the world's floras of gymnosperms and ferns and even more gradually evolved into groups recognizable as extant families and genera. About 15 million years of slow angiosperm evolution took place before diverse angiosperm floras, like the Dakota, Potomac, and Cheyenne Sandstone floras, came into prominence by Upper Albian time, perhaps 112 million years ago (Wolfe *et al*, 1976). Not until the Turonian and Senonian, 100 to 90 million years ago, were gymnosperm pollen and fern spores over-taken in abundance in the fossil record by angiospermous pollen. By late Senonian time, perhaps 70 million years ago, angiosperms had largely replaced the ferns and gymnosperms (Muller, 1970, Wolfe, 1974, Wolfe *et al*, 1976). Possibly modern orders had appeared some tens of millions of years earlier. Many modern families and most extant genera have not been recognised from the fossil record until Tertiary times in the last 65 million years, and many taxa still have no acceptable fossil record.

Probable Angiosperm Ancestors

Our knowledge of the morphology of various vascular plant classes has now enabled us to narrow down considerably those primitive vascular-plants groups that might have evolved into the early angiosperms. Pteridophytes, confers, ginkgoes, cycads, gnetophytes, and the extinct Cordaitales and Bennettitales have now been removed from consideration, largely because they are more specialized in certain features than those archaic angiosperms now generally regarded as the most primitive living flowering plants (Eames, 1961; Cronquist, 1968; Takhtajan, 1969). The most primitive gymnosperms, the extinct Pteridospermae or seed-ferns, still remain as possible ancestors because of their generally primitive characteristics and their great diversity. Most recently Stebbins (1974) has revived rather unconvincingly the hypothesis that the angiospermous ovule is homologous with the seed-bearing cupule of the advanced Mesozoic pteridosperm order Caytoniales. However, the fossil Caytoniales, like the eliminated vascular-plant groups listed above, appear to be too specialized to pass as angiosperm ancestors. It seems more likely that some little-known, or probably still unrecognized, unspecialized group of Mesozoic seed-ferns evolved very early in the Cretaceous into the first angiosperms.

Where these long-extinct, unspecialized pteridosperms presumably evolved into recognizable angiosperms is also still controversial. At best, we can make an educated guess as to the probable centre of evolution of the Angiospermae by assembling what we know of the probable habitats of the earliest flowering plants and of fossil and extant distribution patterns of the most primitive living angiosperms.

Tropical Character of the Angiospermae

Most angiosperm families are basically tropical in their adaptations and their geographic distribution. In an analysis of the 316 families accepted in my classification (Thorne, 1968, 1974), I have found 167 to have an exclusively or primarily tropical distribution, 106 a strong, or nearly equal, representation in both tropical and temperate zones, and only 43 an exclusively or largely temperate distribution. Of the 43 temperate families only four, Adoxaceae, Butomaceae s.s., Hippuridaceae, and Myzodendraceae, each represented by a single genus, are primarily cool temperate in distribution, although two subfamilies, *Hectorelloideae* and *Tetrachondroideae* are essentially subantarctic in range. Every one of the 43 temperate families appears to be related to families that are primarily tropical and that are less specialized in many features, i.e., more primitive. If additional subfamilies are tallied with the families, 314 families and subfamilies are primarily tropical, 204 both tropical and temperate, and only 101 primarily temperate. The tropical bias of the Angiospermae thus is readily evident, approximately three to one. The families generally considered most primitive in the class are even more strikingly tropical. Analysis of the 95 families of the relatively primitive superorders Annoniflorae, Theiflorae, Rutiflorae, and Hamamelidiflorae shows 57 primarily tropical and only 11 largely temperate, a ratio of more than five to one.

Angiosperm megafossil evidence, according to Axelrod (1959, 1970) indicates that the first recognizable flowering plants appeared from equable, warmer uplands first in lower middle latitudes at the beginning of the Early Cretaceous (Neocomian time), where they made up a very small percentage of the total vascular plant flora. At that time they were unrepresented in the megafossil record at high latitudes. As Axelrod graphically shows, they appeared at higher latitudes in progressively younger rocks until by late Cretaceous time they had in great variety largely replaced pteridophytes and gymnosperms even at higher, temperate latitudes. By Aptian time according to megafossils, angiosperms were present south of the equator only in lower latitudes. By the end of the Early Cretaceous in the Albian stage they had reached 70° N latitude but were only beginning to appear at middle latitudes (45° S) in the southern hemisphere (Axelrod, 1959). Fossil pollen evidence seems to support only in the broadest way this apparent poleward migration of early angiosperms (Doyle, 1969; Brenner, 1976; Hopkins, 1974). From this data, we can infer that the Angiospermae evolved in tropical areas, probably north of the equator.

Mesic Origins of the Angiospermae

Perhaps even stronger than the fossil evidence are the inferences we can draw from extant archaic angiosperms, those relicts with vesselless xylem or with extremely primitive tracheid-like vessel elements that are long and narrow and have long scalariform perforation plates with usually more than 20 bars. These woody plants, like broad-leaved conifers, are essentially restricted to highly mesic sites with a minimum of seasonal water stress, primarily tropical montane forests or summer-wet temperate forests (Carlquist, 1975). This is a devastating argument against Stebbins' recently enunciated hypothesis (1974) that the first angiosperms were shrubby plants that evolved in response to a stressful warm climate with distinct dry and wet seasons. It was only as the angiosperms evolved xylem with greater conductive efficiency that they were able to invade and radiate rapidly in the hot tropical lowlands with their wide fluctuations in soil moisture and high insolation, and the temperate forests with more seasonal water stress (Carlquist, 1975). The extreme plasticity of both dicotyledons and monocotyledons allowed many of them rather early in their evolution to adapt to extreme habitats and unusual life-styles (Hickey, 1971; Doyle and Hickey, 1972; Doyle, 1973).

Thus the evidence from both fossil and extant primitive angiosperms indicates that they arose in continuously moist, tropical or subtropical uplands. Indeed, it is in just such montane areas today that we find the great majority of the angiosperms with a wide array of primitive features in flowers, pollen grains, seeds, and fruits as well as in stem anatomy, habit, and foliage. But we still have to decide which moist equable upland area is the probable original homeland of the primitive living Angiospermae.

Possible Centre of Origin of Primitive Angiosperms

Southeastern Asia and its adjacent archipelagoes have most often been suggested by plant geographers as not only the most important centre of preservation but also as the likely "cradle" of the Angiospermae (Takhtajan, 1957, 1969; Thorne, 1963; Smith, 1970, 1973). Recently, however, the general acceptance of the theory of tectonic plate movement and sundering and floating apart of continents has caused some plant geographers to reconsider the problem with view to the suggested distribution of land masses during Cretaceous and early Tertiary times. Schuster (1972) and Raven and Axelrod (1974) favour Gondwanaland as the area from which the initial radiation of the angiosperms took place. The latter authors, on what often appears to be negative evidence, favour West Gondwanaland (South America and Africa as a unit), while claiming unconvincingly that the Oriental Region could not be the area of origin of the angiosperms because of its presumed composite Continental origin.

Oriental Region

We should, therefore, examine the flora of the Oriental Region, which I define here as tropical southeastern Asia and the adjacent Indian-Western Pacific Ocean archipelagoes from Ceylon and Taiwan to tropical Queensland and Fiji. Few plant geographers would deny that this region has the world's most varied flora. Though smaller than the Ethiopian and Neotropical Regions, it possesses indigenous representatives of 433 major angiospermous taxa (families and additional subfamilies), 45 of them endemic, as compared to 366 major taxa, 38 endemic, for Madagascar and Africa south of the Sahara Desert, and 374, with 25 endemic, for all of South America including Fuegia. Among the most primitive angiosperms, the Annonales, Berberidales, Nymphaeales, and Hamamelidales, representation in the Oriental Region is even more overwhelming: 29 of 34 major annonalean, 15 of 18 berberidalean, 6 of 6 nymphaealean, and 11 of 11 hamamelidalean taxa. The same distribution pattern with the most primitive members of the taxon restricted to the Oriental Region is repeated in major taxon after major taxon. Takhtajan (1969) has given many examples. Some of the additional tropical groups that appear to have evolved primarily in southeastern Asia are the thealean *Dillenoideae*, Actinidiaceae, Dipterocarpaceae, Nepenthaceae, and *Planchonioideae*; Ericaceae; Symplocaceae; *Rafflesioideae*; Elaeocarpaceae; *Ficus*; *Gonystylus*; *Cardiopteris*; Rutaceae; Sabiaceae; *Acer*; Juglandineae; Fagales; Staphyleaceae; Daphniphyllineae; Crypteroniaceae; *Astronioideae*; *Cyrtrandroideae*; Rhizophoraceae; Cornineae (except *Garrya*); Caprifoliaceae; orchidaceous *Apostasiodeae* and *Cypripedioideae*; Pandanaceae; and Zingiberaceae.

That the Oriental Region is of composite Continental origin may well be true. It is widely claimed that India-Ceylon split away from Africa and Madagascar at least 100 million years ago, colliding with Asia 45 m. y. BP, and that Australia broke away from Antarctica about 49 m. y. BP, arriving in its present position near Indonesia some 15 m. y. BP (Raven and Axelrod, 1975). Assuming that this time-table is correct, even 15 million years is surely more than adequate time to explain the widespread Indo-Malesian elements that dominate the rain-forest flora of tropical Queensland, New Guinea, and the other Melanesian islands. The flora of distinctive relicts of Australasia that Raven and Axelrod seem to attribute to Gondwanaland are more likely Oriental derivatives which have found a refuge in the isolated islands and highlands of Australasia. *Degeneria*, *Galbulimima*, and *Eupomatia* are very close relatives of the Magnoliaceae, of which all 12 genera and most of the perhaps 215 species are represented in mainland southeastern Asia or the Malay archipelago. The recently rediscovered *Idiospermum* of Queensland belongs to the Calycanthaceae (Thorne, 1974), whose other two genera, *Calycanthus* and *Chimonanthus*, are both represented in China. *Amborella*, *Austrobaileya*, and the Trimeniaceae have close relationships to the Calycanthaceae and to the Chloranthaceae and Monimiaceae, both heavily represented in the Indomalaysian area. Possibly the Winteraceae, with chief centres of variation in New Guinea and New Caledonia may be autochthonous relicts of Australasia but they have relatively close affinities with the Oriental Illiciineae and Magnoliineae. The only two hamamelidalean genera of Queensland, *Ostrearia* and *Neostrearia* of the Hamamelidoideae, have undoubtedly reached northern Queensland, like *Distyliopsis* in New Guinea, from southeastern Asia, where their probable two closest relatives *Embolanthera* and *Maingaya* occur along with representatives of the other four subfamilies and a total of 15 of the 27 hamamelid genera, 4 more being found in temperate Asia. It is noteworthy that like the rain-forest angiosperm flora of New Guinea, New Caledonia, and tropical Queensland, most of the insect, land snail, oligochaete, avian, bat, and murid rodent faunas, at least of New Guinea and the tropical rain forests of Queensland, are derived from southeastern Asia or Malesia (Gressitt, 1956, 1961; Solem, 1958, 1959; Keast, 1959; Emerson, 1955; Mayr, 1972; Schodde and Calaby, 1972). For these reasons in my biogeographical subdivision of the Pacific islands (1963) I treated New Guinea, the Bismarck, Admiralty, and

Solomon Islands, wet tropical Queensland, and New Caledonia as the Papuan and Neocaledonian subregions of the Oriental Region. I do not think a Gondwanic origin of Australia-New Guinea has had much impact upon the majority of angiospermous elements of the tropical rain forests of Australasia.

West Gondwanaland

The importance of West Gondwanaland and other tropical areas in the evolution of the tropical angiospermous flora must not be ignored, however. The Cretaceous angiosperms, according to the fossil record, radiated evolutionarily and geographically very widely and rapidly. Before West Gondwanaland disintegrated into the modern widely separate austral continents, it was probably the centre of origin of the tropical Annoniaceae; Scytopetalaceae; Sapotaceae; Euphorbiales; Geraniales; Caricaceae; Hydnoraceae; Chenopodiaceae; the rosalean Chrysobalanaceae, Connaraceae, *Caesalpinoideae*, *Mimosoideae*, and Podostemaceae; liliacean *Haemodoreae*, *Hypoxidoideae*, *Velloziaceae*, and Iridaceae; Areciflorae; and Musaceae, among others. A longer list can be gleaned from Raven and Axelrod (1974), but it must be used with caution since they claim a Gondwanic origin for taxa that are and were apparently meagrely represented there if at all.

South America

After the break-up of Gondwanaland, the ancient shield areas of South America, especially the Guayana Highlands and Brazilian Planalto, appear to have contributed heavily to the development of such important tropical groups as the thealean *Bonnetioideae*, *Pelliceroideae*, Marcgraviaceae, Caryocaraceae, Saraceniaceae, Quinaceae, and *Lecythidoideae*; Theophrastaceae; cistalean *Peridiscus*, *Leoniaceae*, and Loasaceae; Solanaceae; *Goupia*; Lissocarpaceae; tiliaceous *Tetralicoideae* and *Neotessmannioideae*; *Houmarioideae*; Polygalaceae; rutalean *Dictylomatoideae*, *Spathelioideae*, and *Alvaradoideae*; centrospermous Cactaceae, Rhabdodendraceae, and *Coccoloboideae*; rubiaceous Henriquezioideae; Martyniaceae; Asteraceae; Cyclanthaceae; commelinalean Bromeliaceae, Pontederiaceae, Juncaceae, Commelinaceae, and Eriocaulaceae; and zingiberalean Heliconioideae, Cannaceae, and Marantaceae.

Africa

On the other hand, Africa seems to have contributed somewhat less to the origins of the tropical flora, perhaps because of the floristic depauperization that Raven and Axelrod (1974) emphasize so strongly. Certainly of African-Madagascan origin are the thealean Scytopetalaceae, Sarcolaenaceae, Sphaerosepalaceae, *Monotoideae*, Dioncophyllaceae, and *Napoleonoideae*; Huacaceae; Barbeyaceae; Didymelaceae; simaroubaceous *Kirkioideae* and *Balanitoideae*; Melanthaceae; centrospermous Aizoaceae and Didiereaceae; rosalean *Jollydoroideae*, *Montinioideae*, and Medusagynaceae; pittosporalean Bruniaceae; myrtalean Oliniaceae and Paenaceae; Pedaliaceae; Hoplestigmataceae; and liliacean *Cyanastroideae* and *Geosiridoideae*.

Australasia

Although Australasia seems to receive little credit as an important centre of evolution from Raven and Axelrod (1974), it has contributed significantly to the origins of the tropical angiosperm flora. Among other groups that had their primary development if not their origin in Australasia are the Winteraceae; Epacridaceae; Goodeniaceae; Stackhousiaceae; *Akania*, Gyrostemonaceae; rosalean *Escalloniaceae*, Cunoniaceae, and *Davidsonia*; Pittosporaceae; Proteaceae; Casuarinaceae; myrtaceous *Leptospermoideae*; Haloragaceae; lamialean *Chloanthoideae* and *Prostantheroideae*; liliaceous *Xanthorrhoeaceae*; Restionaceae; Centrolepidaceae, and the poaceous *Micrairoideae*.

North America and Temperate Eurasia

North America and temperate Eurasia appear to have contributed few major groups to the tropical angiospermous flora, despite their formerly rich tropical floras. The highlands of Mexico and the Greater Antilles may have contributed to the tropical flora Cyrillaceae, Polemoniaceae, Fouquieriaceae, *Chitonioideae*, *Eriogonoideae*, Crossosomataceae, *Echeverioideae*, Garryaceae, and the liliaceous *Agavoideae*. The total elimination of tropical elements from Europe removes that area from consideration until the fossil record of its tropical epochs is better known.

LITERATURE CITED

- AXELROD, D. I. 1959. Poleward migration of early angiosperm flora. *Science*, N.Y. **130**: 203-207.
- 1970. Mesozoic paleogeography and early angiosperm history. *Bot. Rev.* **36**: 277-319.
- BRENNER, G. J. 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. Pp. 23-47. In C. B. Beck (Editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York. 341 pp.
- CARLQUIST, S. 1975. *Ecological Strategies of Xylem Evolution*. Univ. Calif. Press, Berkeley, Los Angeles, London. 259 pp.
- CRONQUIST, A. 1968. *The Evolution and Classification of Flowering Plants*. Houghton Mifflin, Boston. 396 pp.
- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. *J. Arnold Arbor.* **50**: 1-35.
- 1973. Fossil evidence on early evolution of the monocotyledons. *Q. Rev. Biol.* **48**: 399-413.
- & L. J. HICKEY. 1972. Coordinated evolution in Potomac Group angiosperm pollen and leaves. (Abstract). *Am. J. Bot.* **59**: 660.
- EAMES, A. J. 1961. *Morphology of the Angiosperms*. McGraw-Hill, New York, Toronto, London. 518 pp.
- EMERSON, A. E. 1955. Geographical origins and dispersions of termite genera. *Fieldiana, Zool.* **37**: 465-521.
- GRESSITT, J. L. 1956. Some distribution patterns of Pacific Island faunae. *Syst. Zool.* **5**: 11-32, 47.
- 1961. Problems in the zoogeography of Pacific and Antarctic insects. *Pacif. Insects Monogr.* **2**: 1-94.
- HICKEY, L. J. 1971. Evolutionary significance of leaf architectural features in the woody dicots. (Abstract). *Am. J. Bot.* **58**: 469.
- HOPKINS, W. S. 1974. Some spores and pollen from the Christopher Formation (Albian) of Ellef and Amund Ringnes Island, and northwestern Melville Island, Canadian Arctic Archipelago. *Geol. Surv. Canada Pap.* **73-12**.
- KEAST, A. 1959. Australian birds: their zoogeography and adaptations to an arid continent. Pp. 89-114. In *Biogeography and Ecology in Australia*. Den Haag: W. Junk.
- MAYR, E. 1972. Continental drift and the history of the Australian bird fauna. *Emu* **72**: 26-28.

- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev.* **45**: 417-450.
- RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Mo. bot. Gdn* **61**: 539-673.
- SCHODDE, R. & J. H. CALABY. 1972. The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. Pp. 257-300. In D. Walker (Editor), *Bridge and Barrier: The Natural and Cultural History of Torres Strait*.
- SCHUSTER, R. M. 1972. Continental movements, "Wallace's Line" and Indo-malayan-Australasian dispersal of land plants: some eclectic concepts. *Bot. Rev.* **38**: 3-86.
- SCOTT, R. A., E. S. BARGHOORN & E. B. LEOPOLD. 1960. How old are the angiosperms? *Am. J. Sci.* **258-A** (Bradley Vol.): 284-299.
- P. L. WILLIAMS, L. C. CRAIG, E. S. BARGHOORN, L. J. HICKEY, & H. D. MacGINITIE. 1972. "Pre-Cretaceous" angiosperms from Utah: evidence for Tertiary age of the palm woods and roots. *Am. J. Bot.* **59**: 886-896.
- SMITH, A. C. 1970. The Pacific as a key to flowering plant history. Univ. Hawaii, Harold L. Lyon Arboretum Lecture **1**: 1-27.
- 1973. Angiosperm evolution and the relationship of the floras of Africa and America. Pp. 49-61. In B. J. Meggers, A. S. Ayensu, & W. D. Duckworth (Editors). *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Inst. Press, Washington, D.C.
- SOLEM, A. 1958. Biogeography of the New Hebrides. *Nature* **181**: 1253-1255.
- 1959. Zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana, Zool.* **43**: 239-359.
- STEBBINS, G. L. 1974. Flowering Plants, Evolution above the Species Level. Harvard Univ. Press, Cambridge, Mass. xviii & 399 pp.
- TAKHTAJAN, A. L. 1957. On the origin of the temperate flora of Eurasia. *Akad. Nauk SSSR* **42**: 1635-1653.
- 1969. Flowering Plants, Origin and Dispersal. Transl. by C. Jeffrey. Oliver & Boyd, Edinburgh. 310 pp.
- THORNE, R. F. 1963. Biotic distribution patterns in the tropical Pacific. Pp. 311-354. In J. L. Gressitt (Editor), *Pacific Basin Biogeography*, Bishop Museum Press, Honolulu.
- 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* **6** (4): 57-66.
- 1969. Floristic relationships between New Caledonia and the Solomon Islands. *Phil. Trans. R. Soc. Lond.* **B 255**: 595-602.
- 1974. A phylogenetic classification of the Annoniflorae. *Aliso* **8**: 147-209.
- WOLFE, J. A. 1974. Fossil forms of Amentiferae. *Brittonia* **25**: 334-335.
- J. A. DOYLE, & V. M. PAGE. 1976. The bases of angiosperm phylogeny: paleobotany. *Ann. Mo. bot. Gdn* **62**: 801-824 (for 1975).